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Research Article

Effect of airflow on overland transport potential of the invasive quagga mussel (*Dreissena bugensis*)

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Abstract

The ability to produce byssal threads enables invasive dreissenid mussels to attach to recreational boat hulls and other equipment. These mussels can be exposed to air during overland transport of recreational boats, which affects their potential to survive transport. Survival during air exposure is determined by a variety of environmental factors such as temperature, relative humidity, shaking and vibrations and the movement of air. This study assessed the influence of air movement on the survival and behavioural changes of the quagga mussel (*Dreissena bugensis*). Survival time decreased significantly when mussels were exposed to a wind speed of 10 and 50 km.h^{-1} compared to standing air survival. Mussel clumps survived significantly longer than mussel individuals. The lethal time of 99% of mussel individuals (LT_{99}) decreased from 29.26 to 18.24 hours when exposed to a wind speed of 50 km.h^{-1}. At a wind speed of 10 km.h^{-1} LT_{99} survival times of mussel clumps (26.94 h) were higher compared to individual mussels (19.76 h). Valve gaping behaviour changed when mussels were exposed to flowing air. Mussels exposed to a wind speed of 10 km.h^{-1} were on average open for 6.41% of the time, whereas in standing air mussels were on average open for 26.78% of the time. These results indicate that air movement has an influence on the survival potential of aerially exposed quagga mussels. Management of invasive alien mussels should take into account that the quagga mussel can survive air exposure with an wind speed of 50 km.h^{-1} over 18 hours when attached to boat hulls. 50% of the mussels can be transported alive for distances over 300 km and 1% of the mussels can be transported alive for more than 900 km. Decontamination of boats and associated equipment will be vital for improved spread-prevention of invasive mussels.

Key words: alien species, dispersal pathway, introduction pathway, valve gaping

Introduction

The quagga mussel (*Dreissena bugensis,* also described as *Dreissena rostriformis bugensis* auct. Andrusov, 1897) is rated among the world's worst invasive alien species by the IUCN (Lowe et al. 2000). The quagga mussel uses byssal threads to strongly attach to a variety of surfaces (Grutters et al. 2012; Matthews et al. 2014). This enables quagga mussels to clog up pipes, to foul ship hulls and to attach to native mussel species, such as unionid mussels (Haag et al. 1993; Strayer 1999). Moreover, quagga

mussels alter macroinvertebrate composition, affect plankton abundance and result in system-wide alteration of water clarity, light penetration and nutrient cycling (Matthews et al. 2014; Karatayev et al. 2015). Costs associated with the quagga mussel and other dreissenid mussels are high, with estimates of damages and management of at least $1 billion/year in the United States (Pimentel et al. 2005).

An important pathway for the introduction of alien species is overland transport of recreational watercraft (Rothlisberger et al. 2010; Bruckerhoff et al. 2015). The rapid range expansion of the quagga mussel is partly due to its attachment to ship hulls and subsequent overland transport (Wilson et al. 1999; Matthews et al. 2014). Their attachment to dispersal vectors allows the species to spread within and between water bodies. Ships not only move through waterways but might also be transported overland amongst isolated water bodies (Buchan and Padilla 1999; De Ventura et al. 2016). In particular, the high level of propagule pressure associated with overland transport of recreational watercraft can further aid the spread and establishment of the quagga mussel (Matthews et al. 2014; Collas et al. 2018).

Survival of mussels during overland transport depends on their tolerance to the acting air temperature and relative humidity (Byrne et al. 1988; Ricciardi et al. 1995; Ussery and McMahon 1995; Snider et al. 2014). Clumped quagga mussels had a higher air exposure survival due to elevated relative humidity concentrations inside the clump (Ricciardi et al. 1995). Air exposed mussels close their valves to reduce water loss and to increase survival (Byrne and McMahon 1994). Valve closure during air exposure results in a switch from an aerobic metabolism to anaerobic (McMahon 1988; Byrne et al. 1990; Davenport and Wong 1992). This anaerobic metabolism can only be maintained for a limited period of time after which mussels display valve gaping to respire aerobically with the trade of off increased water loss potentially leading to mortality. Thus valve gaping behaviour could mediate an increased overland transport survival of the quagga mussel, aiding its spread.

During overland transport of a watercraft, the attached mussels are not just exposed to air but also to vibrations and airflow, which can further affect their survival. However, the effect of the airflow (*viz.* the movement of air) on the aerial exposure tolerance of dreissenids has only been assessed for *Dreissena polymorpha* (Pallas, 1771) by Ussery et al. (1998). They found a decrease in survival of air exposed zebra mussels that colonised a PVC pipe at an airflow of 6.5 $km.h^{-1}$ compared to standing air conditions. Negative effects of airflow on survival of bivalves have also been found for the marine bivalves *Modiolus modiolus* (Linnaeus, 1758) (Coleman 1973) and *Lasaea rubra* (Montagu, 1803) (Kensler 1967), underpinning the importance of including airflow effects in desiccation experiments. The mechanism for the increased mortality of *M. modiolus* was an increase in water loss from tissues, ultimately resulting in dehydration (Coleman

1973). The increase in water loss during exposure to airflow was imminent in individuals that displayed valve gaping, underpinning the effect of valve gaping on mussel survival during air exposure.

This study focusses on the effect of airflow on potential survival of the quagga mussel during ship hull-mediated overland transport. Based on the decreased survival during moving air exposure of the zebra mussel found by Ussery et al. (1998) we hypothesize that air movement decreases survival of the quagga mussel and hence reduces their overland dispersal potential. We expect that higher wind speeds decrease survival further. Contrary, mussel clumps are hypothesized to be less affected by airflow than individual mussels due to an elevated relative humidity within clumps (Ricciardi et al. 1995) and a sheltering of the direct effects of airflow. Gaping behaviour under airflow conditions is expected to be reduced to minimize the risk of dehydration.

Materials and methods

Experimental set-up

Quagga mussels were collected on the 18th of April and 6th of May 2019 in impounded sections of the river Meuse near the municipality of Mook (51°44′29.2″N; 5°53′00.7″E) and the river Nederrijn near the municipality of Lexkesveer (51°57′34.1″N; 5°41′21.9″E). Mussels were sampled through carefully slicing the byssal threads using a knife after which they were transferred to containers with aerated water from the collection site. Collection time was limited to one hour. Thereafter the mussels were brought within 20 minutes to a climate chamber with a constant temperature of 18.8 °C. Mussels were kept at a density that was lower than under field conditions in order to prevent limitation of food. The acclimatisation time prior to any experiments was at least 24 hours. To minimize potential confounding effects of mussel collection on experimental results, only mussels that showed signs of filtration activity were used in experiments. Using the mussels from the river Meuse, two experiments were performed to assess: 1) the effect of air movement on mussel survival, and 2) the effect of mussel clumps on air movement survival. Larger mussels collected at the river Nederrijn were used to assess valve gaping behaviour during exposure to various airflow conditions. All experiments were performed in a climate chamber with a constant temperature of 18.8 °C and an average relative humidity of 76.8% (ranging between 72 to 88%). Survival rates during experiments were determined after 24 hours of immersion. A mussel was classified as dead, according to Paukstis et al. (1999) when stimulation of the mantle did not result in shell muscle contraction.

Air movement

Individual mussels (Experiment 1)

The effect of air exposure on the survival of individual mussels was studied at an air speed of 10 and 50 km.h^{-1}. The same set-up but without air movement

Table 1. Overview of the number of *Dreissena bugensis* individuals, number of groups and experimental duration used during exposure of individual mussels (experiment 1) and mussel clumps (experiment 2) to standing air, or a wind speed of 10 km.h^{-1} or 50 km.h^{-1}.

Experiment	Treatment	No. of groups	Median group size	Range group size	Experimental duration (h)
1. Individuals	Control	18	10	always 10	0; 2; 4; 6; 8; 12; 16; 20; 24; 28; 29.5; 30; 32; 36; 40; 42; 46; 48
	10 km.h^{-1}	20	10	always 10	0; 1; 2; 3; 4; 5; 6; 7; 8; 12; 16; 18; 20; 22; 24; 26.5; 28; 32; 42; 48
	50 km.h^{-1}	13	10	8–11	0; 0.5; 1; 2; 3; 4; 5; 6; 7; 14; 18; 22.5; 24
2. Clumps	Control	16	10	9–14	0; 2; 4; 6; 8; 16; 20; 24; 28; 32; 40; 44; 48; 56; 64; 72
	10 km.h^{-1}	15	12	8–21	0; 2; 3; 6; 8; 16; 20; 24; 28; 32; 40; 44; 48; 64; 72
	50 km.h^{-1}	11	10	3*–17	0; 0.5; 1; 2; 3; 4; 5; 6; 7; 14; 28

* Two groups were partially blown away by the force of the wind speed resulting in a group of 3 and 6 individuals, the minimum group size excluding these groups was eight.

was used as a control treatment. For this control treatment, 18 groups of 10 individual mussels were placed in front of a fan without turning the fan on. For the 10 km.h^{-1} and 50 km.h^{-1} treatments, the number of groups was 20 and 13, respectively. All groups of the 10 km.h^{-1} treatment consisted of 10 individuals. For the 50 km.h^{-1} treatment group size ranged between 8 and 11 individuals with a median of 10 individuals. A total of 476 mussels was used in the experiment with individual mussels. At the start of the experiment, mussels were placed in metal slots made of wire to prevent mussels from being blown away (Supplementary material Figure S1). Subsequently, each group of mussels was exposed to the experimental treatments for a set duration ranging between 1 to 48 hours (Table 1). The shell length of the mussels ranged between 5.2 to 14.9 mm with an average of 10.5 mm.

Mussel clumps (Experiment 2)

Survival of mussel clumps was assessed during wind exposure at a speed of 10 and 50 km.h^{-1}. The same set-up but without air movement was used as a control treatment. For this control treatment 16 clumps ranging between 9 and 14 mussels were placed in front of a switched off fan. For the 10 km.h^{-1} and 50 km.h^{-1} treatments, the number of clumps was 15 and 11, respectively. Clump size of the 10 km.h^{-1} treatment ranged between 8 and 21 individuals. Like experiment 1, clumps were placed in metal slots made of wire to prevent mussels from being blown away (Figure S1). Despite use of metal slots, individuals from two clumps of the 50 km.h^{-1} treatment were blown away resulting in a remaining clump of 3 and of 6 individuals, respectively. For the other clumps in the 50 km.h^{-1} treatment clump, size ranged between 8 and 17 individuals with a median of 10 individuals. A total of 443 mussels was used in the experiment with mussel clumps. Subsequently, each clump was exposed to the experimental treatments for a set duration ranging between 1 to 72 hours (Table 1). The shell length of the mussels ranged between 4.0 to 18.6 mm with an average of 10.2 mm.

Valve gaping (Experiment 3)

Valve gaping measurements were performed using a Hall sensor that measured changes in the electromagnetic field due to increasing or decreasing distance between valves (Wilson et al. 2005; Gnyubkin 2009). The frequency of the electromagnetic field was set at 100 Hz to obtain sufficient detail in valve gaping behaviour (Robson et al. 2009). The Hall sensor was glued to one shell of the mussel and the magnet to the other shell. Subsequently, the mussel was exposed to either standing air or flowing air (10 $km.h^{-1}$) for six hours. The experiment was performed using 16 mussels per treatment. Mussels had a shell length ranging between 14.8 to 17.7 mm with an average of 16.1 mm.

Data analysis

A binomial generalized linear model (GLM) was used to analyse the effect of "time" (continuous variable) and the categorical variable "wind speed" (0 $km.h^{-1}$, 10 $km.h^{-1}$ and 50 $km.h^{-1}$) and "cluster" (individuals and clump) on the fraction of surviving individuals. The analysis were performed using the GLM function in R statistics (R core Team 2019). Several models were fit (Table S1), after which model selection was based on the lowest Akaike's information criterion (AIC) value. The best performing model included the main effect of "time", "wind speed" and "cluster" and the two-way interaction between "time" and "wind speed" and "time" and "cluster". Tukey post-hoc analyses were performed using the "lsmeans" function from the "lsmeans" package (Lenth 2016). The two clumps exposed to a wind speed of 50 $km.h^{-1}$ with individuals that were blown away were maintained in the data analysis since the survival at the time before and after these two clumps yielded similar survival rates. The average shell size of each group and group size were not included in the model as no observable patterns were detected in relation to group survival. After the GLM was fitted the lethal time until 50% and 99% mussel mortality (LT_{50} and LT_{99}, respectively) was derived using the MASS package in R statistics (Venables and Ripley 2002).

The valve gaping data of each individual mussel was used to determine 1) the timing of the first valve gaping event (in milliseconds after experimental start), 2) the number of valve gaping events, and 3) the percentage of time that the mussel was gaping during the experiment. A valve gaping event was classified as the moment when the voltage of the Hall sensor decreased with at least 40 mV. This threshold value was chosen based on observations during a trial run. A GLM with a gamma distribution was fitted using data on timing of the first valve gaping event with treatment as a categorical variable. The frequency of valve gaping events and the percentage of time that a mussel was gaping were not characterized by a distinct distribution. Therefore, the conservative non-parametric Kruskal-Wallis rank sum test was used to identify significant differences of these indicators between

Table 2. GLM results of quagga mussel survival during air exposure experiments with "time" included as a continuous variable and "air speed" and "cluster" as categorical variable and their interaction.

Source	Df	Deviance	Resid. Df	Resid. Dev.	P-value
Survival					
NULL			92	890.5	
Time	1	695.41	91	195.09	< 0.001
Wind speed	2	49.87	89	145.22	< 0.001
Cluster	1	22.86	88	122.35	< 0.001
Time: Wind speed	2	7.55	86	114.8	< 0.05
Time:Cluster	1	6.2	85	108.59	< 0.05

Df: degrees of freedom; resid. Df: residual degrees of freedom; resid. dev: residual deviance.

treatments. In both analyses "treatment" was used as a categorical variable. Two mussels were found to be glued shut and were therefore removed from the analyses.

Results

Air movement

A significant relationship between exposure time and mussel survival was found (Table 2). The effect of time significantly differed between wind speed treatment (Table 2). Post-hoc analyses showed that the effect of time on mussel survival was significantly higher during the 10 and 50 $km.h^{-1}$ treatment compared to the standing air treatment (p-value < 0.001 and 0.01, respectively; Figure 1A and B). No significant difference was found regarding the effect of time between the 10 and 50 $km.h^{-1}$ treatment (p-value = 0.85). Air exposed mussel individuals were more quickly affected by time than mussels grouped in clumps (Table 2). The best model excluded the three way interaction "Time" × "Wind speed" × "Cluster", indicating that the effect of wind speed was consistent for both individual mussels and mussel clumps (Figure 1A and B).

Under the standing air, both the LT_{50} and LT_{99} value were higher for the mussels in clumps than individual mussels (Table 3). When wind speed was 10 $km.h^{-1}$ and 50 $km.h^{-1}$ the LT_{50} values for both mussels clumps and individual mussels reduced by 40 and 47%, respectively. LT_{50} values of mussel clumps exposed to 10 $km.h^{-1}$ and 50 $km.h^{-1}$ wind speed reduced by 48 and 54% compared to the standing air treatment (Table 3). For both the mussels clumps and individual mussels the fivefold higher wind speed at 50 $km.h^{-1}$ did not result in a fivefold decrease in LT_{50} and LT_{99} values but in 12.1 and 12.6%, respectively (Table 3).

Valve gaping

At the end of the experiment six mussels in each treatment were dead. Two mussels with an air movement treatment were removed from the analyses because their valves were glued shut. No significant differences between the two treatments were found regarding 1) the timing of the first opening

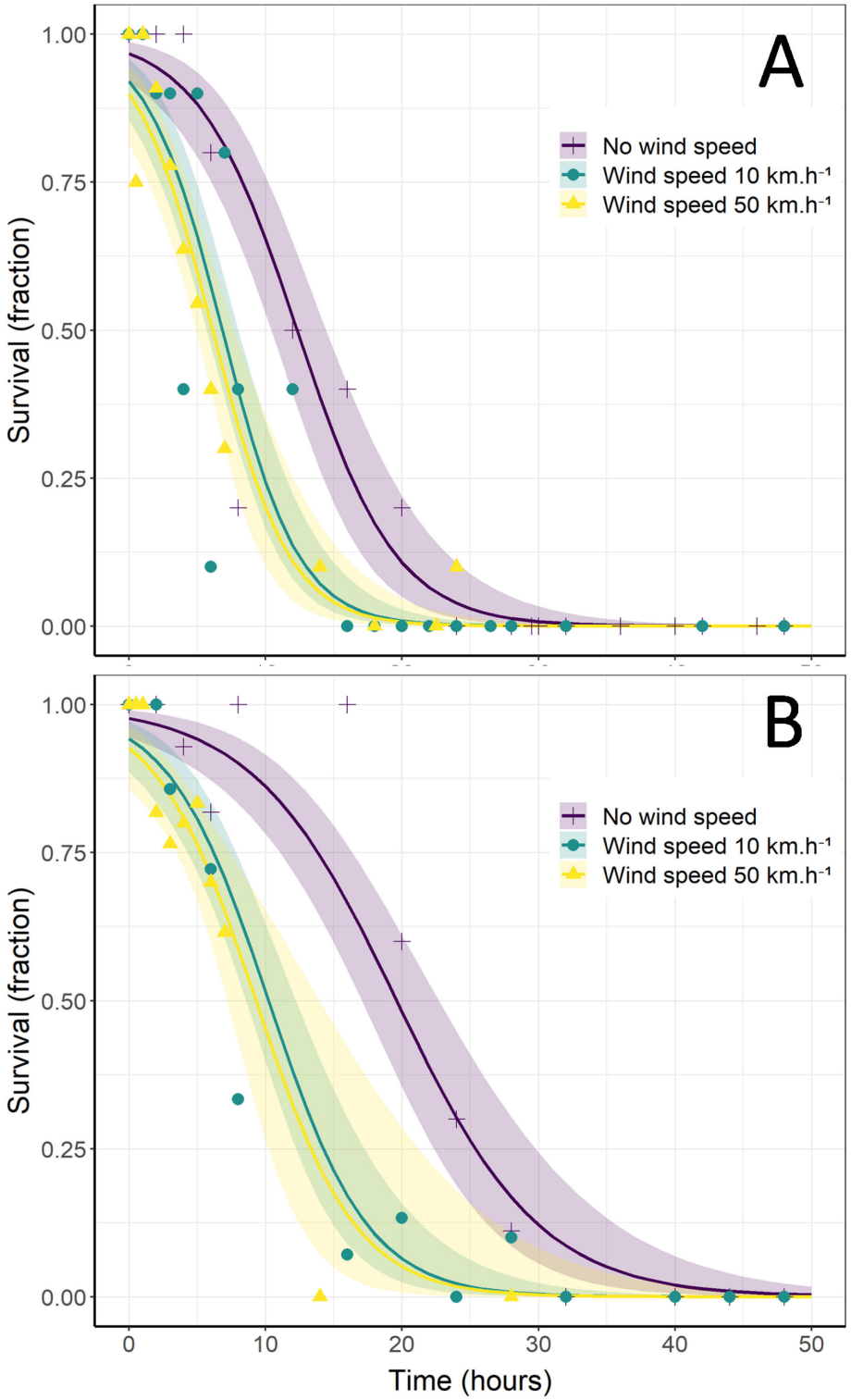

Figure 1. Effect of standing air and airflow of 10 km.h^{-1} or 50 km.h^{-1} exposure on the aerial survival of (A) individual mussels and (B) mussel clumps of *Dreissena bugensis*.

event (t-value = 1.100; df = 20; p-value = 0.2844), and 2) the number of valve gaping events (Kruskal-Wallis χ^2-value = 2.1729; df = 1; p-value = 0.0995). A significant difference in the total duration of valve gaping in treatments with and without airflow was found (Kruskal-Wallis χ^2-value = 6.873; df = 1; p-value < 0.01; Figure 2).

Table 3. The time until 50 and 99% mortality of *Dreissena bugensis* (LT_{50} and LT_{99}) when exposed as either individual mussels or mussel clumps to standing air, or an airflow of 10 km.h^{-1} or 50 km.h^{-1}. For each combination of lethal time and airspeed the potential dispersal distance was calculated.

Treatment		Survival endpoint (hours)		Potential dispersal distance (km)	
		LT_{50} (± SE)	LT_{99} (± SE)	LT_{50}	LT_{99}
Individuals	No wind speed	11.37 (± 1.95)	29.26 (± 5.61)	n.a.	n.a.
	10 km.h^{-1}	6.84 (± 1.76)	19.76 (± 5.15)	68.4	197.6
	50 km.h^{-1}	6.01 (± 1.73)	18.24 (± 5.07)	300.5	912
Clumps	No wind speed	19.55 (± 2.32)	43.62 (± 6.61)	n.a.	n.a.
	10 km.h^{-1}	10.21 (± 1.97)	26.94 (± 5.74)	102.1	269.4
	50 km.h^{-1}	8.92 (± 1.92)	24.51 (± 5.59)	446	1225.5

n.a.: not applicable.

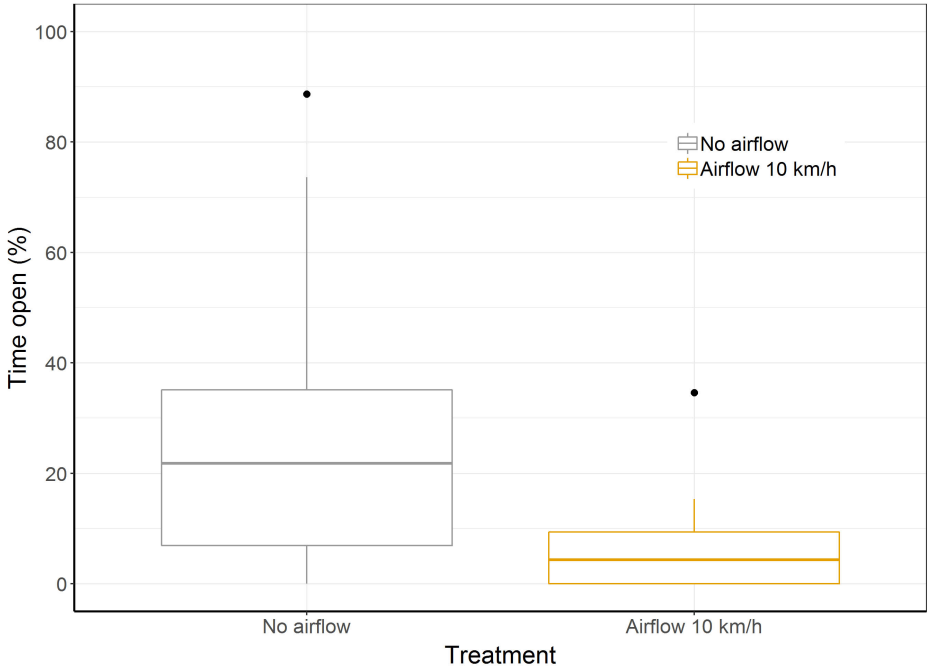

Figure 2. Whisker plots of the duration of valve gaping of *Dreissena bugensis* exposed to standing air and an airflow of 10 km.h^{-1}. The bands in the middle of the box represent the median and the lower and upper bands of the boxes are the 25th and 75th percentiles, respectively. The upper and lower whiskers were derived using the standard settings in R statistics and the dots represent outliers.

Discussion

Air movement

Air movement during emersion of *D. bugensis* affects their survival potential. The LT_{50} and LT_{99} values decreased with air movement speed. This confirms our hypothesis that air movement increases the mortality of *D. bugensis*. The results correspond with Ussery et al. (1998), who found that moving air reduced the LT_{50} of *D. polymorpha* at 25 °C with 10.3 hours. Moreover, Coleman (1973) found that standing air exposure of *M. modiolus* for 6 hours did not lead to mortality, whereas mussels exposed to airflow died within 1 hour of exposure. For all three species, a decreased survival has been found due to airflow, suggesting that this is a generic

effect for all freshwater bivalves. Future research on the potential effect of droughts on mussel survival should therefore take airflow into account.

Under field conditions, dreissenids tend to be aggregated in clumps when attached to ship hulls (Keevin et al. 1992). Our results show that mussel clumps have a longer survival time during air exposure than individual mussels, though airflow resulted in a larger decrease in LT_{50} and LT_{99} for mussel clumps than individual mussels. The clump size used in our experiment was low and thus likely overestimates effects on survival since bigger clumps retain more moisture (Ricciardi et al. 1995). However, the positive effect on survival of mussels in larger clumps is countervailed, as these clumps are more likely to detach than small ones due to shakings and wind surges during overland transport. All LT_{50} values were higher than 6 hours and all LT_{99} values were higher than 18 hours, even at wind speeds of 50 $km.h^{-1}$. The latter implies that 1% of the attached mussels on boat hulls could survive an over-land transport of circa 900 km. Apart from the boat-hull mediated pathway, boats have also been found to transport mussels and veligers through any form of water carried by boats (e.g., in live wells, engines; Johnson et al. 2001).

Contrary to our hypothesis, higher wind speeds did not result in decreased quagga mussel survival. The effect of a five-fold increase in airspeed (10 $km.h^{-1}$ to 50 $km.h^{-1}$) did not result in a five times lower survival. Thus, there does not appear to be a linear relation between airflow survival and wind speed. However, under natural circumstances trailered mussels are expected to be exposed to higher speeds (*viz.* higher wind speeds) as the maximum travelling speeds of cars with trailers in the European Union ranges between 70 and 130 $km.h^{-1}$ (ANWB 2020). The available experimental set-up did not allow assessing the effect on quagga mussel survival at such air speeds. The effect of air movement on the LT_{50} and LT_{99} at higher speeds is expected to reduce survival times of *D. bugensis* and the potential human assisted dispersal of this species by boat-hull mediated overland transport. Moreover, vibration of boats on trailers play a role in survival of mussels during overland transport. It is possible that vibrations enhance the probability of detachment and reduce the potential of their overland spread (Collas et al. 2018).

Valve gaping

Our study shows that *D. bugensis* exposed to airflow spend significantly less time gaping compared to the standing air treatment. There are multiple factors that play a role in survival during flowing air exposure which may have led to the found difference in valve gaping behaviour, such as the build-up of an oxygen debt during anaerobic metabolism (Akberali and Trueman 1985) but also the evaporation of water during valve gaping resulting in weight loss (McMahon and Payne 1992; Ricciardi et al. 1995). Without airflow, survival is the result of the interplay between their aerobic

and anaerobic metabolism and the build-up of harmful end products (McMahon 1988). Though, with air movement, evaporation of water in air exposed mussels strongly increases (Coleman 1973). At an wind speed of 13 km.h^{-1}, the average weight loss of *M. modiolus* after six hours was 28% compared to 16% during standing air conditions. Coleman (1973) found that exposure for 6 hours to standing air did not result in mortality nor in a high water loss. *Modiolus modiolus* mussels exposed to airflow conditions were characterized by a high water loss and died within 1 hour of exposure. Preliminary results of a study on exposure of quagga mussels to an airspeed of 6 km.h^{-1} at 10 °C also showed an increase in weight loss (*unpublished results*). This effect of airflow on water loss implies that a short-term reduction of evaporation during airflow conditions becomes more urgent than limiting the long-term effects of an increased oxygen debt. In addition, the airflow itself is expected to increase the efficacy of flushing of air inside the mussel resulting in a reduced gaping duration to offset the negative effects of an anaerobic metabolism (Byrne and McMahon 1994). Future studies should focus on this possible trade-off in more detail, as it might provide a more fundamental explanation for survival rates of mussels during overland transport or water-level drawdowns in rivers and lakes (Leuven et al. 2014; Collas et al. 2020).

The valve gaping results are biased towards larger individuals as sufficient size was needed to glue on the hall-sensors. When exposed to air, smaller *D. polymorpha* were found to have a higher weight loss compared to larger individuals (Ricciardi et al. 1995). Thus, smaller quagga mussels are expected to show an even further reduced valve opening time under airflow conditions. Additional airflow experiments with smaller mussels regarding valve gaping will provide results that match with the mussel size of 4 to 16 mm found on boats by Karatayev et al. (2013).

Survival during the valve gaping experiment is overestimated due to the limited experimental duration of six hours. Therefore, it is recommended to use longer experimental durations in future research. An interesting observation was that some of the mussels that displayed opening and closing behaviour right until the end of the experiment where found to be dead after the subsequent 24 hours of immersion. This suggests that the measured behavioural responses were sub-optimal since mortality of these individuals was not avoided. A potential sub-optimal behavioural response of some of the experimental animals could mean that we underestimate the effect of airflow on the total duration of valve gaping.

Management implications

Air movement and clumping of mussels proved to be important factors to take into account in future ship hull-mediated overland dispersal assessments. Differences in their survival can be explained by differential strategies in gaping behaviour. *Dreissena bugensis* survives exposure to air

movement speeds of 50 km.h^{-1} for more than 18 hours. This supports that *D. bugensis* can spread into isolated water-bodies via the boat hull-mediated pathways (Minchin et al. 2003; De Ventura et al. 2016; Collas et al. 2018). This potential for human-assisted dispersal implies that good biosecurity practices are imperative to prevent further overland spread of the species, such as extensive cleaning and prolonged drying of boat hulls (Clean Boating Act 2008). Other biosecurity practices that could be applied are antifouling coatings, disinfectants, steam, hot air, hot water, high pressure washing and dry ice (Minchin et al. 2006; Rothlisberger et al. 2010; Comeau et al. 2011; Watters 2014; Joyce et al. 2019; Coughlan et al. 2020).

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Constructed cages used to make sure that the mussels exposed to air movement would not be blown away.
Table S1. Fitted models with included main effects and interactions and the corresponding Akaike's information criterion value on which final model selection was based.

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